Seasonal Variation in the Song of Male House Wrens (*Troglodytes aedon*)

Honors Research Thesis

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Abstract

In songbirds, male song is a major component of courtship display and mate attraction. Previous studies suggest that male song may serve to attract females for extra-pair copulations, during which a mated male seeks additional females for mating purposes outside of the pair bond. If song is used to attract additional mates, the song output of the male bird should fluctuate very little throughout the breeding cycle. The purpose of this study was to determine how the song of male house wrens (*Troglodytes aedon*) fluctuates throughout the breeding season. House wrens are socially monogamous, but have high levels of extra-pair paternity. Fifteen minute recordings of male song were obtained throughout the breeding season and were analyzed for changes in rate, duration, and frequency. While song characteristics do not vary with date, both song length and song rate declined during the nestling feeding stage compared to egg-laying and incubation stages. These results may indicate that gaining a monogamous partner is of greater importance in male house wren reproductive success than is gaining extra-pair partners.

Introduction

Sexual selection can lead to evolution via male-male competition and female mate choice. Male-male competition, or competition between the males of a species for access to the females of the same species (Lifjeld et al. 1994), often facilitates female mate choice, or female selection of mates based on male quality (Eckerle and Thompson 2005). One way to assess male quality is via courtship displays.

In songbirds, male song is a major component of courtship display and mate attraction. Female attraction to male song components such as song rate and length has been observed in species such as northern cardinals (*Cardinalis cardinalis*; Ritchison 1988), eastern bluebirds (*Sialia sialis*; Huntsman and Ritchison 2002), and whitethroats (*Sylvia communis*; Balsby 2000).

Birds are one of the most diverse groups in terms of the range and variety of songs produced by males to attract a mate.

Male bird songs are series of complex and often musical vocalizations used during the breeding season in an effort to advertise availability to females (Scheiber 2001). Studies have shown that the patterns and frequency of male song change with respect to the breeding cycle, and several non-mutually exclusive hypotheses exist to predict at which point in the breeding cycle male song rate will be at its peak (Johnson and Kermott 1991).

One such hypothesis is the mate guarding hypothesis, which predicts that male song output should be greatest during the paired female's fertile period (Møller 1988). This hypothesis has been supported in many bird species, including the dusky warbler (*Phylloscopus fuscatus*; Forstmeier and Balsby 2001) and the tropical boubou (*Laniarius aethiopicus*; Grafe and Bitz 2003).

An alternative hypothesis is the mate attraction hypothesis, which predicts that male song output should be greatest prior to obtaining a mate (Johnson and Kermott 1991). This hypothesis has also been supported for many species of birds, including chipping sparrows (*Spizella passerine*; Albrecht and Oring 1994) and reed buntings (*Emberiza schoeniclus*; Brunner and Pasinelli 2010). In the study conducted by Albrecht and Oring (1994), the researchers saw the highest average singing rates just prior to mate pairing, confirming the mate attraction hypothesis. Brunner and Pasinelli (2010) saw similar results, and also observed that the maximum frequency and the complexity of the male song (i.e. the average number of syllables and different types of syllables used) were greatest prior to mating.

In the context of the mate attraction hypothesis, it has also been suggested that male song may serve to attract females for extra-pair copulations, rather than simply attracting a single mate

(Møller 1988). Extra-pair mating involves one or both members of a mated pair seeking mating opportunities outside of the pairing (Poirier et al. 2003). Bearing this in mind, it is possible that male bird song has a three-fold purpose: (1) to attract an initial mate, (2) to guard the mate during her fertile period, and (3) to attract additional mates for extra-pair copulation. In this scenario, the song output of the male bird should remain high and fluctuate very little throughout the breeding cycle; constant song output would be required to keep the bird as attractive as possible to as many mates as possible.

The house wren (*Troglodytes aedon*) is an ideal species for studying the role of male bird song as it relates to the breeding cycle. House wrens are small songbirds found throughout northwest Ohio that show moderate levels of extra-pair mating (Poirier et al. 2003). One study of house wrens showed that approximately 55% of all surveyed individuals participated in extra-pair mating during the breeding season (Drilling and Thompson 1991). This study is being conducted in order to determine how the song of male house wrens fluctuates throughout the breeding season. We hypothesize that the song rate (number of songs per given time period), song length, mean frequency, and maximum frequency of male song will fluctuate very little throughout the breeding cycle as a result of the high likelihood of achieving extra-pair copulations. In order to mate outside of the monogamous pair, the male will need to stay as attractive as possible to other females; this is presumably accomplished by continuous advertisement through song.

Methods

Study area and recordings

This study was conducted from April to August 2011 in Lima, Allen County, Ohio, USA (Figure 1). Prior to wren arrival in April, 123 nest boxes were erected in one of three habitats: a

woodland habitat on the Ohio State University at Lima campus (40 boxes; 40.7363927° N, -84.0266254° W), a residential/industrial area near the campus (43 boxes; 40.747556° N, -84.034588° W), and a public golf course (40 boxes; 40.752005°N, -84.036931° W). Nest boxes were checked twice weekly prior to nesting, and daily during egg laying and hatching periods in order to determine the exact day of egg laying and hatching.

Three stages of the breeding cycle were targeted for recordings: laying (4 eggs or fewer in the nest), incubation (days 5-7 from the time the last egg was laid), and nestling feeding (day 4 after >50% of the eggs had hatched). At each stage, the male was targeted for 30 continuous minutes of recording. Recordings were obtained between 0600 and 1200 hrs and were made using a Marantz PMD-660 digital recorder and an Audio Technica shotgun microphone. The microphone was attached to the supporting pole of the nest box, and pointed straight up. The date, box number, and start time were noted at the start of each recording. The recorder level and speaker volume were standardized for each recording session.

Data analysis

Program Signal (Version 4.04.29, Cambridge Electronic Devices 2008, Cambridge, UK) was used to measure song rate, song length, mean frequency, and maximum frequency for a selected fifteen minute period of each song recording. Each fifteen minute period was chosen from the point at which the focal male first began singing. Song length, mean frequency, and maximum frequency were measured only for songs that were clearly recorded (little background noise) using a customized program within Program Signal developed by D. Nelson (unpub. data). If a song occurred, but there was interference from background noise, the song was noted for the total number of songs in 15 min, but length and frequency were not measured. Song rate, song length, mean frequency, and maximum frequency were averaged for each time period.

Program JMP (Version 9.0.0, SAS Institute Inc. 2010, Cary, NC) was used to compare reproductive stage (laying, incubation, and nestling feeding) with song rate, song length, mean frequency, and maximum frequency. Sample sizes vary because it was not possible to obtain song recordings from every male.

Results

Between June and August of 2011, 102 recordings of male song were obtained from 44 nests. Between 38-58% of nests at each location were sampled (woods: 19 of 33 nests; golf course: 20 of 52 nests; residential area: 5 of 11 nests). Those nests not sampled were initiated before we could obtain recordings or failed before we could obtain recordings. Additionally, some nests failed following initial recording, so a complete set of recordings (during laying, incubation, and nestling feeding) could not be obtained.

Male house wren song consists of a series of low amplitude notes resembling a chatter followed by several high amplitude notes (Figure 2). Within the 102 recordings obtained during this research, 2063 individual songs were analyzed with an average of 19 ± 6 songs per 15-minute recording. The average length of wren song was 1.47 ± 0.12 s. The mean frequency of wren song was 4.10 ± 0.08 kHz. The average maximum frequency of wren song was 5.81 ± 0.13 kHz.

Song characteristics varied with nest stage, but not date or time. For songs recorded during the laying stage, the song rate, song length, mean frequency, and maximum frequency did not vary by day within season or time of day (all $P > 0.30$, $F_{2, 43} < 1.12$). The song rate increased between the laying and incubation stages (matched pairs: $t = -2.68$, df = 28, $P = 0.01$) and decreased between the incubation and nestling feeding stages ($t = -2.14$, df = 20, $P = 0.04$; Figure 3). There was no change in song length between the laying and incubation stages

(matched pairs: t = 0.86, df = 17, P = 0.40), but a decrease in song length between the incubation and nestling feeding stages (t = -2.59, df = 14, P = 0.02; Figure 4). Mean frequency did not change between the laying and incubation stages (matched pairs: t = -1.16, df = 17, P = 0.26), or between the incubation and nestling feeding stages (t = -0.91, df = 13, P = 0.38). Maximum frequency did not vary between the laying and incubation stages (matched pairs: t = -0.41, df = 17, P = 0.68) or between the incubation and nestling feeding stages (t = -1.44, df = 13, P = 0.17).

Discussion

Both song length and song rate declined with nest stage (although song rate increased between the laying and incubation stages, the overall trend was downward [see Figure 3]). Similar results were seen by Johnson and Kermott (1991), who showed that high volume spontaneous song in house wrens sharply declined following pairing. Johnson and Kermott also noted that song output increased only when a male lost a mate, which may explain the high song output seen in the later breeding stages of certain males during this experiment. Studies of song sparrows (*Melospiza melodia*; Foote and Barber 2009) and stonechats (*Saxicola torquata*; Greig-Smith 1982), which, similarly to house wrens, are socially monogamous, also saw a decline in the rate of male song from incubation to nestling feeding stages. One study by Slagsvold (1976) correlated the song output of more than twenty species of birds to stage of the breeding cycle; song output declined with both season and breeding stage.

Changes in the frequency of male song over the course of the breeding season were not seen most likely as a result of the need to maintain interspecific recognition. According to Kroodsma (1973), interspecific recognition is facilitated by similarities in species characteristics, such as behavior or morphology. In birds, behavioral similarities may be manifested through

song (Kroodsma 1973), providing a possible explanation for a consistent range of vocal frequencies seen throughout house wren populations. A study of two populations of house wrens in Argentina and Oregon found that male song characteristics such as duration and syllable usage varied little (Tubaro 1990), suggesting that additional song elements such as frequency range may be maintained for interspecific recognition. The average maximum frequency of song found during this study (5.81 ± 0.13 kHz) was comparable to the 4.8 kHz average maximum frequency found during a study of male house wrens in Wisconsin (Platt and Ficken 1987).

The tendency for total song output to decline with nest stage, particularly between incubation and nestling feeding stages, suggests that maintaining a monogamous partner may be of greater importance in male house wren reproduction than is gaining extra-pair partners. Studies of several bird species, including Carolina wrens (*Thryothorus ludovicianis*; Strain and Mumme 1988) and European starlings (*Sturnus vulgaris*; Wright and Cuthill 1992), have noted the importance of song rate in initial pairing success. Song is energetically very costly (Eberhardt 1994). As both male and female house wrens feed the young (Poirier et al. 2003), a male must allocate energy between offspring care and mate attraction. A study by Poirier (2003) noted that male house wrens who participated in extra-pair copulations did not further their reproductive success when compared to males who did not participate in extra-pair copulations. If reproductive success is indeed not furthered by extra-pair copulations, a male maximizes his reproductive success by allocating energy to his monogamous mate and her offspring. The need for the male to continually advertise through song once he has paired is therefore greatly reduced, as the data obtained during this project suggest. Future studies may benefit from recording the songs of male house wrens over the course of several breeding seasons in order to

determine how song fluctuates from year to year, as mate availability may also fluctuate yearly (Poirier et al. 2003), requiring more or less advertisement by a male.

Continuation of this research would benefit from beginning recording sessions earlier in the breeding season. While June through August mark the peak of the breeding season, many wrens return to nest in late April and early May. Obtaining recordings earlier in the year would increase the sample size, furthering the emergence of any trends in the data. Continued research may also benefit from recording the song of male wrens prior to pairing, as male song output may be greatest prior to obtaining a mate (Albrecht and Oring 1994). This study was limited to studying male song output after a male had already obtained a mate. Based on nesting data recorded during this project, a nest box containing approximately 2-3 cm of nesting material indicates an unpaired male that is soon likely to obtain a female (nest construction progresses rapidly after this point, with the formation of the nest cup indicating that the male has paired), making it an ideal point at which to record pre-pairing song.

In summary, advertisement through song is a major component of male courtship display in birds. In some birds, male song is used to attract females for the purpose of extra-pair copulations. In the case of house wrens, the data obtained in this experiment suggest that male song output is greatest when seeking to attract a monogamous mate. Male house wrens may maximize their reproductive success through monogamy and parental care rather than through attempts at extra-pair paternity.

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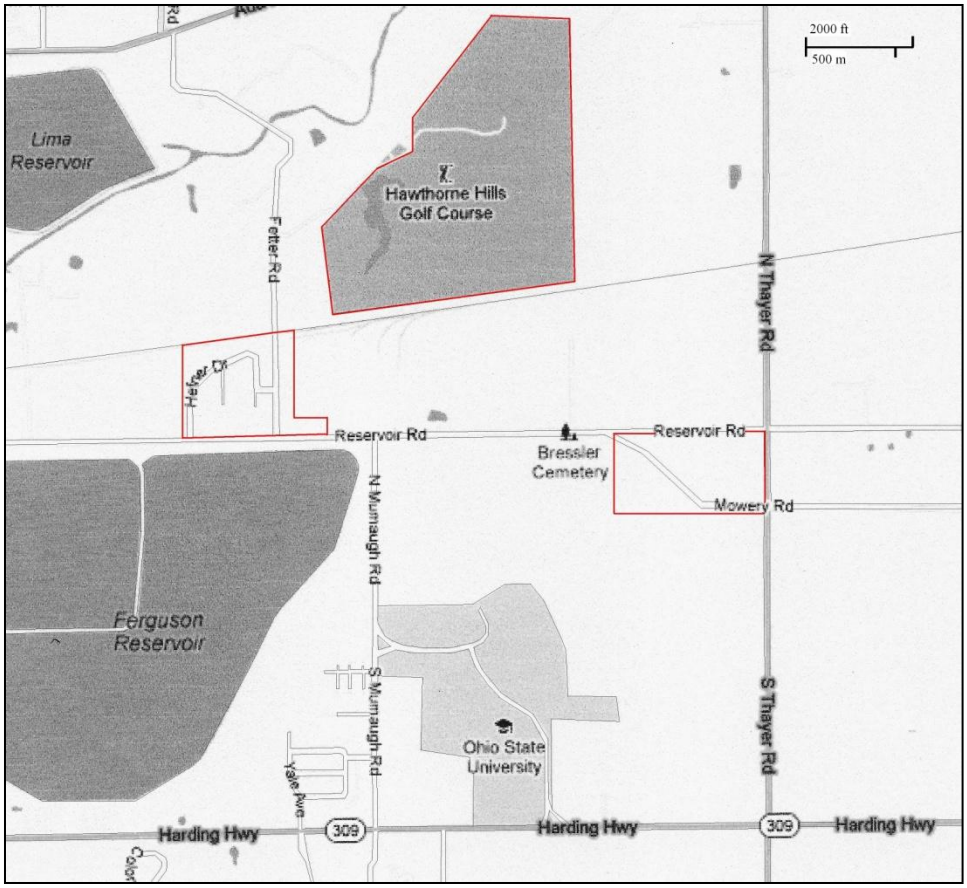

FIGURE 1: Map of the study areas outlined in red (courtesy of Google Maps).

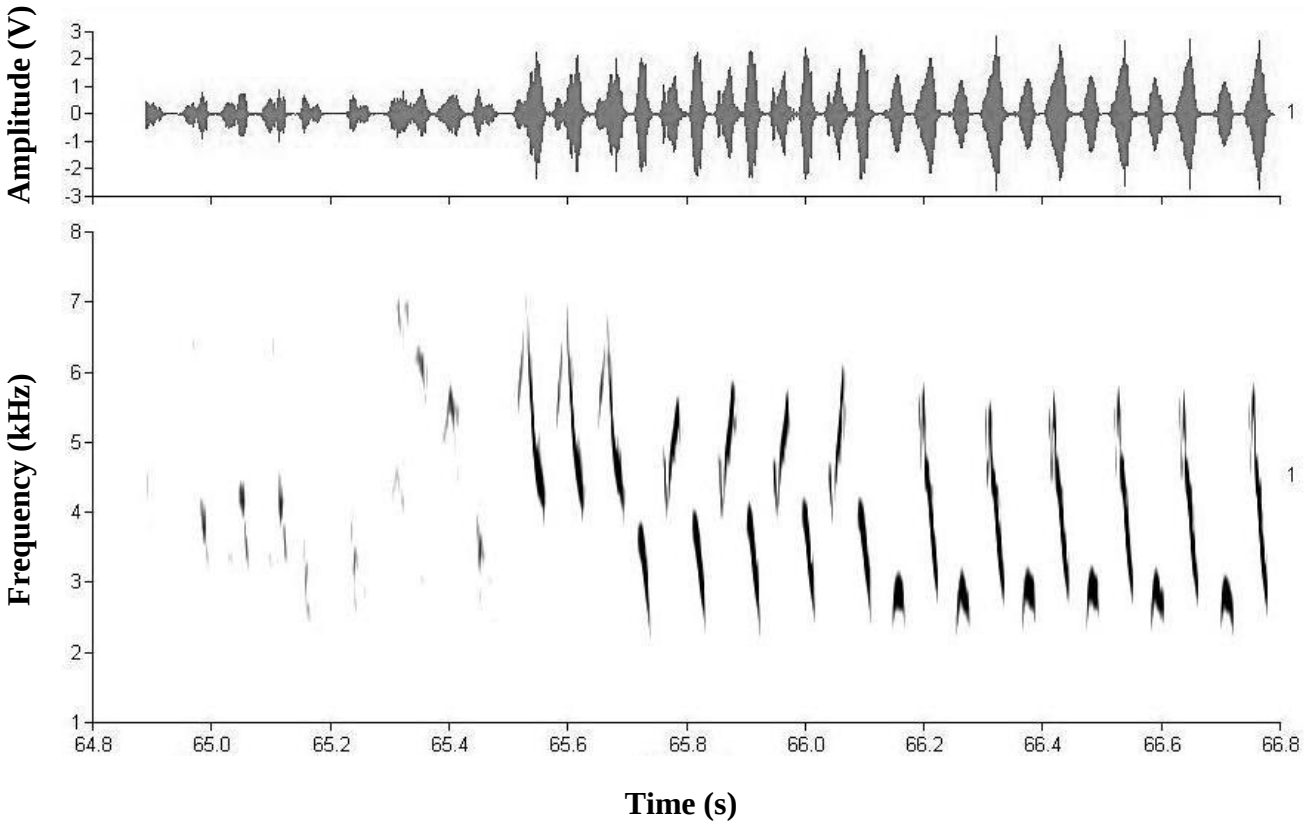

FIGURE 2: Sonogram of a typical male house wren song in Allen County, OH, June-August 2011.

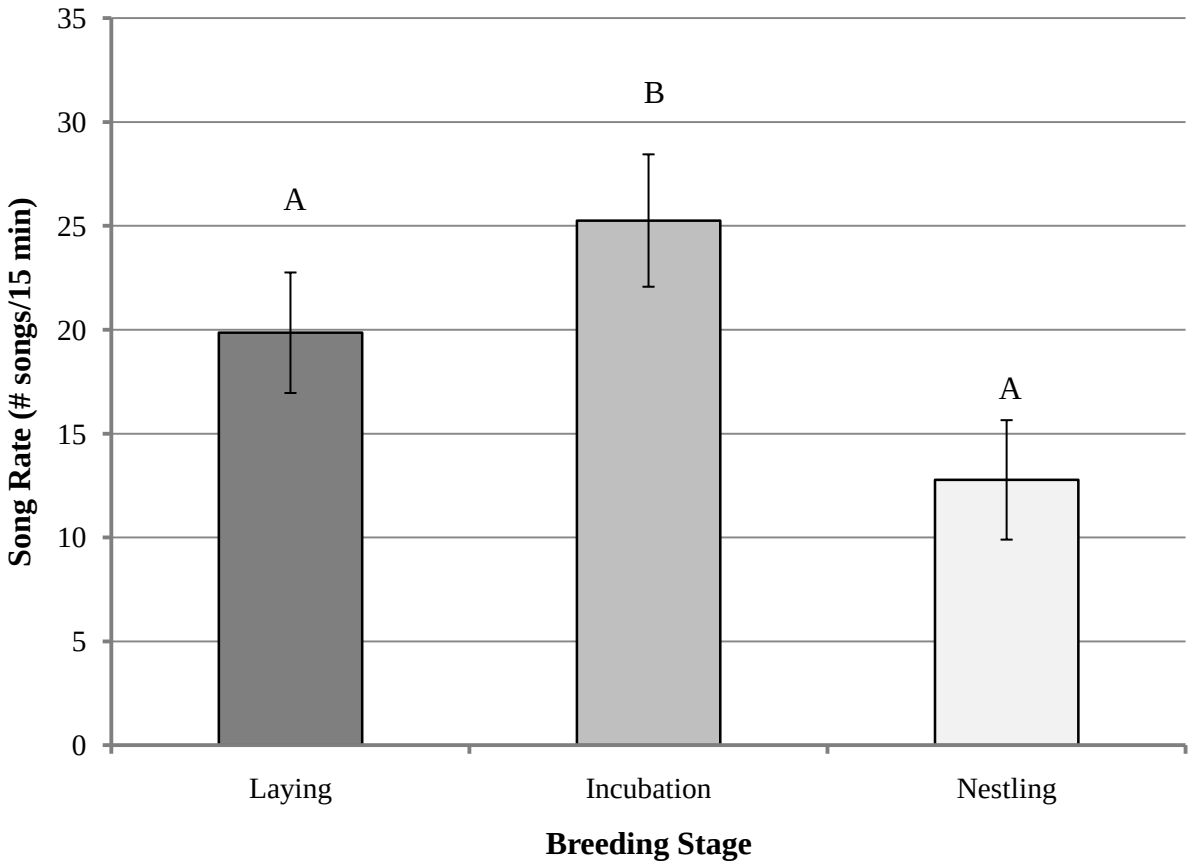

FIGURE 3: The relationship between breeding stage and song rate of male house wrens in Allen County, OH, June-August 2011. Different letters represent significant differences ($P < 0.05$) using a matched-pairs analysis.

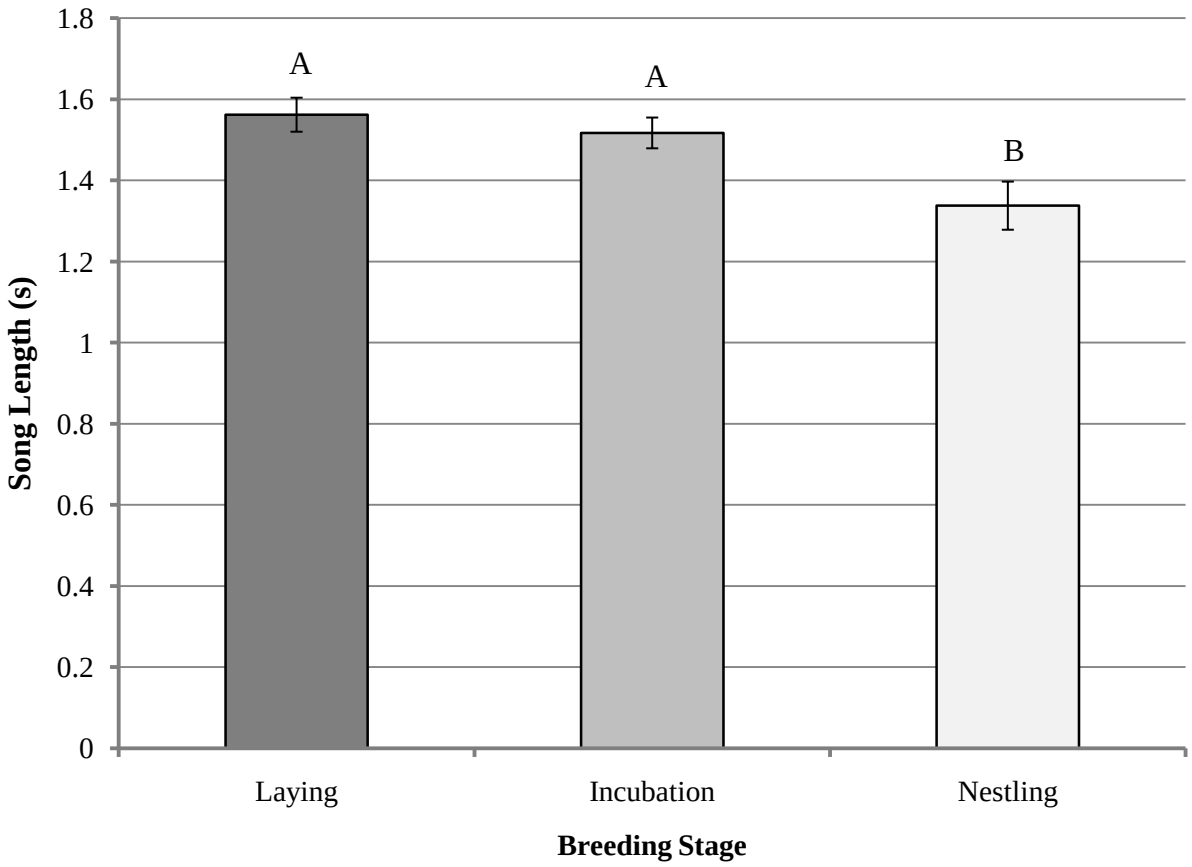

FIGURE 4: The relationship between breeding stage and song length of male house wrens in Allen County, OH, June-August 2011. Different letters represent significant differences ($P < 0.05$) using a matched-pairs analysis.